

20. Effects of Aluminum on Plant Growth

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I. ALUMINUM TOXICITY IN SOILS

A. Occurrence and Importance

ALUMINUM toxicity is an important growth-limiting factor in many acid soils (Adams and Pearson, 1967). The problem is particularly serious in strongly acid subsoils that are difficult to lime (Adams, 1968, 1969; Adams and Lund, 1966), and it is being intensified by the heavy use of acid-forming nitrogen fertilizers (Abruna *et al.*, 1958; Pearson *et al.*, 1962; Wolcott *et al.*, 1965; Pierre *et al.*, 1971). Aluminum toxicity is also increased by the addition of nonnitrogenous fertilizers that displace exchangeable Al into the soil solution and lower soil pH even more (Ragland and Coleman, 1962). Strong subsoil acidity, with Al at toxic levels, reduces root penetration and increases the probability of injury by drought, a frequent growth-limiting factor for crops, even in the humid eastern United States. In acid soils Al is toxic as a cation, but aluminate (anion) toxicity has also been reported in alkaline fly ash deposits of England (Jones, 1961).

B. Soil Factors Affecting Aluminum Toxicity

The solubility of Al and the severity of its toxicity to plants are affected by many soil factors, including soil pH, type of predominant clay mineral, concentrations of other cations, total-salt concentrations, and organic matter content.

In general, Al toxicity does not occur in soils above pH 5.5 (McCart and Kamprath, 1965), but it is common at lower pH values, and parti-

cularly severe below pH 5.0, where the solubility of Al increases sharply (Magistad, 1925) and more than half the cation exchange sites may be occupied by Al (Evans and Kamprath, 1970). For example, Adams (1968) reported that cotton (*Gossypium* sp.) roots failed to proliferate in subsoil of pH 5.0 or below, growth was stunted, and plants wilted during midseason within 3 to 4 days after a rain. On the other hand, when the subsoils were within the pH range of 5.2 to 5.5, subsoil rooting occurred, yields were not reduced, and plants could withstand drought periods of 10 to 14 days without wilting.

For a given acid soil, lime responses of crops are often well correlated with the KCl-exchangeable Al levels (Table 20.1; Moschler *et al.*, 1960; Abruna-Rodriguez *et al.*, 1970; Kamprath, 1970; Foy *et al.*, 1965a), but the soil pH at which Al becomes soluble in toxic concentrations is different in different soils. Hester (1935) found that the pH at which plant growth was markedly inhibited in Coastal Plains soils coincided with that at which Al appeared in soil drainage water. Soils having colloids of low silica : sesquioxide ratios (Norfolk) produced Al toxicity at higher pH values than those with higher ratios (Bladen). These critical pH values were 4.8 for Portsmouth, 4.9 for Bladen, and 5.5 for Norfolk. In support of Hester's conclusions, Adams and Lund (1966) reported that the displaced solution of a Norfolk subsoil contained toxic levels of Al for cotton at a soil pH of 5.4, but Bladen subsoil did not contain toxic levels above pH 4.9. The critical soil pH for primary cotton root penetration was about 5.5 for Norfolk subsoil and less than 5.0 for Dickson and Bladen subsoils. In recent field studies with cotton and corn (*Zea mays*), Adams (1968, 1969) also demonstrated that certain soils of the Coastal Plains differ in "critical" pH, the maximum pH at which a given crop responds to lime.

Table 20.1. Effects of lime on the top growth of Hudson barley and on the pH and level of KCl-extractable Al in Tatum surface soil

CaCO ₃ added (ppm)	Yield of barley tops (g/pot)†	Soil properties‡	
		pH	KCl-extractable Al (meq/100 g)
0	0.29 e	4.1	5.75
375	0.91 d	4.3	4.81
750	2.72 c	4.5	4.33
1,500	4.29 b	4.8	2.75
3,000	5.07 a	5.5	0.37

Source: Foy *et al.*, 1965a.

† Values having different letters are significantly different at the 5% level by Duncan's Multiple Range Test.

‡ Averages of three replicates.

Adams and Lund (1966) found that the levels of exchangeable Al required for toxicity were also quite different in different soils, being 0.1 meq/100 g for Norfolk, 1.5 for Dickson, and 2.5 for Bladen. Thus, Al is toxic at a higher soil pH level and at a lower level of exchangeable Al in Norfolk subsoil, whose predominant clay mineral is kaolinite, than in Dickson and Bladen, whose major clay mineral components are vermiculite and montmorillonite, respectively. These investigators concluded that the soil pH, exchangeable Al, and degree of Al saturation were not satisfactory indicators of root growth inhibition in several Coastal Plains soils. In addition, they found that no single critical Al concentration in displaced soil solutions would apply to all the soils studied. For example, an Al concentration of 0.013 meq/l in Bladen subsoil solution was more toxic to roots than was 0.042 meq/l in Dickson subsoil solution, even at lower pH levels in Dickson. However, placing soil solution Al on a molar activity basis resulted in similar critical values for all soils. Cotton root penetration was restricted at values above 0.15×10^{-5} for both displaced soil solutions and the nutrient solution portion of a split medium. They attributed the lower toxicity of Dickson soil solution to a higher salt concentration which reduced the activity coefficient of the Al. Increasing the calcium concentration of a nutrient solution, at the same initial pH, is known to reduce the toxicity of Al and other excess cations (Table 20.2; Foy *et al.*, 1969; Wallace *et al.*, 1970; Lund, 1970).

Richburg and Adams (1970) concluded that differences in critical pH values of soil were caused both by differences in $\text{Al}(\text{OH})_3$ activity and by differences in the relationship between the pH of soil-water suspensions and the pH of displaced soil solutions. For example, Lucedale soil, which had a critical pH of 5.1, had higher $\text{pAl}(\text{OH})_3$ values than those of Norfolk and Magnolia (critical pH 5.5). The Lucedale subsoil also had the highest displaced solution pH; a soil suspension of pH 5.1 in all three soils produced displaced soil solution pH values of 5.1 in Norfolk, 5.2 in Magnolia, and 5.5 in Lucedale.

Organic soils are known to have lower critical pH values for good crop growth than mineral soils (Welch and Nelson, 1950). The addition of humic acid lowers the pH at which plants are injured in certain acid soils (Mattson and Hester, 1933) and prevents Al toxicity of alfalfa (*Medicago sativa*) in nutrient solutions (Brogan, 1967). Hester (1935) found that the detoxification of Al by the addition of organic matter to acid soils was associated with decreased Al solubility. Evans (1968) reported that Al solubility is very low at pH 5.0 in organic Coastal Plains soils. Bhumbla and McLean (1965) suggested that the exchange acidity displaced at higher soil pH values in some soils is due to organic complexed Al or hydroxy Al polymers. The evidence indicates that the lower critical pH values for plant growth in organic soils compared

Table 20.2. Effects of Al on soybean taproot growth as modified by Ca concentration in the subsurface nutrient solution portion of a split medium

Al added (ppm)	Root elong. rate (mm/hr)†			Harvested root length (mm)			Dry root wt (mg/mm)	
	10 ppm Ca‡	40 ppm Ca‡	10 ppm Ca†	10 ppm Ca	40 ppm Ca	10 ppm Ca	10 ppm Ca	40 ppm Ca
0	2.71	2.86	376	445	0.28	0.38		
0.5	1.88	2.72	295	443	0.27	0.36		
1.0	0.44	2.61	59	427	0.61	0.31		
2.0	0.24	1.57	40	245	0.67	0.40		
LSD 5%	0.38	0.38	115	56				
1%	0.57	0.57	174	84				

Source: Adapted from Lund, 1970.

† Elongation rate during first 48 hours in solution.

‡ Calcium levels were studied in two separate experiments.

with mineral soils is due, at least in part, to the formation of Al-organic matter complexes of lower solubilities (Schnitzer and Skinner, 1963; Greene, 1963; Evans, 1968). However, there is also the possibility that Al is detoxified by chelation in water-soluble forms. For details on the chemistry of Al in soils, see reviews by Coleman and Thomas (1967), and Coulter (1969), and Chapters 15 and 16 of this volume.

II. EFFECTS OF ALUMINUM ON PLANT GROWTH

A. Beneficial Effects of Aluminum

Although Al is generally regarded as a nonessential element, during the past 60 years various claims have been made for its beneficial effects on plants when used at low concentration. Stoklasa (1911) found small quantities of Al beneficial and believed it to be a catalytic agent in photosynthesis; however, higher concentrations coagulated plant proteins and caused a loss of calcium and potassium from the injured cells. Varvarro (1912) reported that aluminum oxide accelerated the germination of corn. McLean and Gilbert (1928) found that 3 to 13 ppm Al stimulated plant growth but higher concentrations were toxic.

MacLeod and Jackson (1965) found that Al concentrations of 0.1 to 0.2 ppm in nutrient solutions increased the growth of alfalfa and red clover (*Trifolium pratense*) seedlings. Aluminum at 5 ppm stimulated the root growth of *Deschampsia flexuosa*, *Alopecurus pratensis*, *Festuca pratensis*, and *Lolium perenne* (Hackett, 1962, 1967). Dios and Broyer (1962) reported that Al stimulated magnesium uptake by corn. Paterson (1965) found that Al at 0.25 to 0.50 ppm stimulated the growth of young corn plants in a Hoagland's solution containing 5 ppm phosphorus at pH 4.1. Bertrand and deWolf (1968) concluded that Al is actually required by corn and specified the optimum dose as 0.25 to 0.30 ppm in nutrient cultures. This corresponds very closely with the findings of Paterson (1965). Growth of the tea (*Thea sinensis*) plant is said to be increased by Al (Goletiani, 1965). Lee (1971b) found that Al at 1 to 5 ppm (pH 3.7) stimulated the vegetative growth and in some cases the uptake of Mg and K by Irish potatoes (*Solanum tuberosum*). In another study Lee (1971a) found that the addition of 20 ppm Al (pH 3.5) decreased the overall yield of potato tubers. All the decreased yield was in the small and knobby potatoes; yield of the larger tubers and the specific gravity of tubers were increased. The mangold (*Beta vulgaris*) plant (an Al-tolerant species) showed increased yields when treated with alkaline fly ash, which contains toxic levels of Al as aluminate (Rees and Sidrak, 1956). Much smaller quantities of ash reduced

yields of Al-sensitive barley (*Hordeum vulgare*). Aluminum added at 2.5 ppm (pH 3.5) stimulated root growth of Al-tolerant cranberry (*Vaccinium macrocarpon*) (Medappa and Dana, 1970). Flower color in *Hydrangea macrophylla* is related to the Al content of the floral tissue (Asen *et al.*, 1963). Blue flowers contain higher concentrations of Al than pink flowers.

The mechanisms by which small quantities of Al benefit plant growth are not clear. A possible explanation is increased iron solubility and availability in the growth medium, resulting from Al hydrolysis and a lower pH. Grime and Hodgson (1969) have presented evidence that the positive Al response of *Scabiosa columbaria* is due to the displacement of Fe (by Al) from bound sites within the plant, thereby relieving an Fe distribution or utilization problem which had caused deficiency.

B. Inhibitory Effects of Aluminum

1. Gross Symptoms of Aluminum Toxicity

Aluminum toxicity in plant tops is often characterized by symptoms resembling those of P deficiency (overall stunting; small, abnormally dark green leaves; purpling of stems, leaves, and veins; and yellowing and death of leaf tips), or of Ca deficiency (cupping or rolling of young leaves and collapse of plant apex or petioles). Recent evidence indicates that bronzing, an important physiological disease of rice (*Oryza sativa*), attributed by some investigators to Fe toxicity (Tanaka and Yoshida, 1970), is actually caused mainly by excess Al in certain soils of Ceylon (Ota, 1968). Velasco *et al.* (1959) noted that high Al levels (which reduce water absorption), plus low copper levels in soils, are closely associated with another physiological disease, kadang-kadang, found in coconut (*Cocos nucifera*) trees in the Philippine Islands.

Aluminum-injured roots are characteristically stubby and spatulate in appearance. Root tips are inhibited and turn brown. The root system as a whole is coralloid in appearance, having many inhibited and thickened lateral roots but lacking in fine branching (Fleming and Foy, 1968; Clarkson, 1969; Reid *et al.*, 1971). Aluminum injury also appears to predispose plant roots to fungal infection (Ota, 1968). Cate and Sukhai (1964) reported that 1 ppm Al had no effect on the germination of rice in Petri dishes but did stunt lateral root growth. Dessureaux (1969) found that up to 100 ppm Al in nutrient solutions did not inhibit the germination of alfalfa but that toxicity began shortly after emergence of the radicle.

2. Cytological Effects of Aluminum

Levan (1945) reported that Al and other salts caused severe cytological abnormalities in the dividing cells of onion (*Allium cepa*) roots, including the formation of "sticky chromosomes" and anaphase bridges. Clarkson (1965) found that Al at 5.4 to 54 ppm, added as $\text{Al}_2(\text{SO}_4)_3$ (pH not given), completely inhibited elongation in onion root after 6 to 8 hours. Cessation of root elongation was closely correlated with the disappearance of mitotic figures. However, other trivalent ions, such as gallium, indium, and lanthanum, produced similar results. Rios and Pearson (1964) observed that Al concentrations above 0.5 ppm (pH not given) prevented growth of cotton seedling roots and that these roots did not recover when placed in Al-free solutions. The appearance of binucleate cells in meristematic regions of root tips indicated that cell division was inhibited. Huck (1972) found that exposing cotton roots to 1 ppm Al (pH 4.3) for 12 hours produced a breakdown of cells in the pericycle and a high frequency of binucleate cells. The Al-damaged tissue was soft and necrotic.

3. Physiological and Biochemical Effects of Aluminum

a. Effects on Protoplasm, Enzyme Activity, and General Metabolism

Many investigators have shown that Al increases the viscosity of protoplasm in plant root cells and decreases overall permeability to salts, dyes, and water (Stoklasa, 1911; Szucs, 1912; McLean and Gilbert, 1927; Hofer, 1958; Bohm-Tuchy, 1960; Aimi and Murakami, 1964). Clarkson and Sanderson (1969) suggested that these effects are due to cross-linking between adjacent protein molecules. Rorison (1958) concluded that Al decreases the extensibility of cell walls by cross-linking pectins in the middle lamella. Aluminum has been shown to accumulate in the nuclei of some Al-injured plant cells (McLean and Gilbert, 1927; Aimi and Murakami, 1964). Avdonin *et al.* (1957) noted that Al decreased the sugar content, increased the ratio of non-protein to protein N, and decreased P contents of leaves from several plants grown on acid podzolic soils. Aluminum toxicity (bronzing) in rice has been associated with interference in the synthesis of starch and protein, reduced translocation of sugars, and increases in the peroxidase and decreases in the cytochrome oxidase activities of leaves (Ota, 1968). Huck (1972) concluded that Al reduced the abilities of cotton roots to utilize sucrose in building cell-wall polysaccharides. Anderson and Evans (1956) found that Fe or Al inhibits isocitric dehydrogenase and malic enzyme activities in bean plants.

Aluminum has been reported to reduce sugar phosphorylation (Rorison, 1965; Clarkson, 1966b), respiration (Norton, 1966–67), and DNA synthesis (Sampson *et al.*, 1965; Clarkson, 1969). Eichhorn (1962) provided evidence that metal cations, which are bound to DNA in vitro, increased the stability of the double helix. On the basis of this evidence, Clarkson and Sanderson (1969) have suggested that the observed interference in DNA replication induced by Al (Clarkson, 1969) takes place by cross-linking of polymers, which increases the rigidity of the DNA double helix.

Progress in discovering the mechanism of Al toxicity has been greatly hindered by the unavailability of a suitable radioactive isotope of Al. Clarkson and Sanderson (1969) noted that at equal concentrations, aluminum and scandium are very similar in their inhibitions of root elongation and cell division and have concluded that ^{46}Sc can reliably indicate the behavior of Al in root meristems. They suggested that these two elements injure plants through a common mechanism which may be more closely related to their polyvalency than to their other properties. However, Clarkson (1969) has also observed that although other trivalent metal ions such as gallium, scandium, yttrium, and lanthanum may produce similar effects on cell division, resistance to Al injury in one species of bentgrass (*Agrostis setacea*) and in rye (*Secale cereale*) appears to be specific and does not necessarily coincide with tolerance to these other ions.

b. Nutrient Uptake and Utilization. Many investigators have associated Al toxicity with reduced uptake of several nutrient elements by plants, particularly Ca and P. However, the question remains: Are these effects intimately involved in the actual mechanism of Al toxicity or merely consequences of an earlier disturbance by Al at the cellular or sub-cellular level?

Reduced Ca uptake is commonly observed in Al-injured plants. For example, Johnson and Jackson (1964) found that Al reduced both the absorption and accumulation of Ca by wheat (*Triticum aestivum*). Paterson (1965) concluded that Al reduced Ca uptake by corn but did not appear to inhibit Ca transport to plant tops. Lance and Pearson (1969) found that Al at only 0.3 ppm in solution reduced Ca uptake by cotton seedling roots within one hour. This inhibition was prevented by increasing the solution Ca concentration to 600 ppm.

Clarkson (1970) found that Al reduced both the Ca associated with the free space of barley roots and the rate at which Ca previously absorbed by cells moved outward across the plasma membrane. He suggested that Al blocks, neutralizes, or reverses the negative charge on the pores of the free space and thereby reduces the abilities of such pores to bind Ca. From this it was postulated that Al should increase

anion binding by the free space and total anion uptake by plants. Data obtained from ^{36}Cl uptake supported the hypothesis.

DeWard and Sutton (1960) associated Al toxicity in black pepper (*Piper nigrum* L.) vines with reduced uptake of Ca and Mg, plant deficiency symptoms of these elements, death of roots, wilting of foliage, and increased uptake of K and Al. They suggested that the ratio of K:Ca plus Mg in plant tops can be used as an index of Al injury. Pepper vines were slightly affected at a ratio of 1.29 and severely affected at a ratio of 3.89.

Aluminum toxicity in rice has been characterized by lower concentrations of Ca, Mg, K, Mn, and Si and higher concentrations of N and P in plant tops (Ota, 1968). Plant injury in rice was positively correlated with Al contents of roots. Lee (1971b) found that Al inhibited the transport of P to potato plant tops; decreased the absorption of Ca, Mg, and Zn by roots; and caused the accumulation of P, Al, Mn, Cu, and Fe in plant roots. Potassium absorption was stimulated by 1 to 2 ppm Al but inhibited by 5 to 10 ppm. Otsuka (1968a) reported that Al induced an Fe deficiency chlorosis in acid-soil-sensitive wheat and barley varieties.

Aluminum reduced the concentrations of Ca, Mg, and K in mature leaves of lettuce (*Lactuca sativa*) and Ca concentrations in all of the leaves (Harward *et al.*, 1955). Total Cu uptake by excised wheat roots was reduced by 0.1 ppm Al in nutrient solutions (Hiatt *et al.*, 1963). The latter investigators suggested that Al was competing with Cu for common binding sites at or near the root surface but not for a common ion carrier involved in active accumulation.

c. Phosphorus Uptake and Utilization. Aluminum toxicity often appears as a P deficiency in plants grown on acid soils or in nutrient solutions (Foy and Brown, 1963, 1964; Chiasson, 1964). Excess Al may reduce the solubility of P in the growth medium and its uptake and utilization by plants. For example, Suchting (1948) found that removing the soluble Al from acid soils increased P recovery of pine trees from 2.5% to 40% of applied P. Increasing the P supply in the growth medium can precipitate and thus detoxify Al, increase P uptake, and prevent P deficiency symptoms. There is also evidence that in the presence of excess soluble Al, a higher level of soluble P is required to prevent P deficiency in cotton (Foy and Brown, 1963).

The detrimental effects of high Al and low P are often extremely difficult to separate in acid soils. However, Reeve and Sumner (1970) concluded that on eight oxisols Al toxicity, P deficiency, and P fixation were primary but independent growth-limiting factors. They attributed the beneficial effects of P fertilization to the elimination of Al toxicity and the resulting increased ability of plants to absorb P, rather than

to increased P availability in soils. Munns (1965a, 1965b) concluded that P treatments reduced the detrimental effects of Al only when they caused Al to precipitate in the medium. He noted that Al decreased P concentrations in both roots and tops of alfalfa but that Al-induced P deficiency symptoms were not corrected by increasing the P level in the growth medium, even when this restored the P concentrations in the plants to high levels. Chiasson (1964) found that in an acid Canadian soil (pH 5.0), banding 20 ppm N and 22 ppm P directly with barley seed prevented leaf-yellowing (P deficiency) symptoms and doubled yields but that lime and MgSO_4 (250 ppm) similarly applied did not influence symptoms or yield. One possible cause of such a beneficial effect is the precipitation of toxic Al by P in the root zone.

In some instances Al toxicity has been associated with reduced P concentrations in both roots and tops (Munns, 1965b). In others Al was believed to precipitate P inside plant roots and thereby cause P deficiency in the tops (Wright, 1937, 1948, 1952). In Wright's studies the P bound by Al-injured roots was largely inorganic and had a low water solubility. He attributed the beneficial effects of large applications of superphosphate on acid soils to precipitation of Al and P inside the plant with sufficient P remaining for metabolic purposes. MacLeod and Jackson (1965) reported that P appeared to be immobilized by Al in alfalfa roots. In contrast to the evidence cited above, Ruschel *et al.* (1968) suggested that the harmful effects of Al on *Phaseolus vulgaris* were not due to an Al-induced P deficiency. Wallihan (1958) concluded that Al did not interfere with P metabolism in ladino clover. Jones (1961) found that S-100 white clover, which he classified as Al-tolerant, accumulated considerable amounts of Al in the leaves but showed little evidence of P deficiency.

Although Al generally reduces the uptake of P by plants, exceptions have been reported. Randall and Vose (1963) found that 5.0 ppm Al in solution culture increased the total P and the P concentrations in both roots and tops of 8-week-old perennial ryegrass plants. Low Al concentrations, given as a pretreatment or during a 4-hour absorption period, greatly increased P uptake. Because this Al-stimulated P uptake was reduced by KCN, they judged it to be connected with metabolism, but they did not rule out precipitation of Al and P on root surfaces. Higher levels of Al (50 ppm) also increased P concentrations in plants but depressed total P uptake by reducing growth. They concluded that Al bound P within the plant and that this produced the P deficiency that they observed. Aluminum-stimulated P uptake has also been found in cranberry (Medappa and Dana, 1968), in excised snapbean roots (Ragland and Coleman, 1962), and in barley seedlings (Clarkson, 1966b). In Clarkson's work the P associated with Al-treated roots was inorganic and almost entirely exchangeable. However, in contrast

to the results of Randall and Vose (1963) with perennial ryegrass, the Al-stimulated P uptake was not reduced by DNP or low temperature, suggesting that the process was not directly dependent upon metabolism.

Rasmussen (1968), using electron microprobe analysis, reported that Al absorbed from acid solutions (as a cation) precipitated on cell walls of corn roots, with no penetration of the cortex as long as root surfaces were intact, but openings made by emerging laterals did provide channels for Al entry. The observation that the distribution of P was exactly the same as that of Al led them to suggest that aluminum phosphate was the precipitate. On the other hand, Waisel *et al.* (1970), using anionic Al (pH 9.5) and X-ray microanalysis, found no correlation between the distribution of Al and P in bean and barley roots. Aluminum appeared to be located inside the cell lumen (with its distribution overlapping that of N), with only trace amounts found in cell walls. The absence of Al precipitates in cell walls suggested to these investigators that the Al in the protoplast was mobile. Differences in the results of Rasmussen (1968) and Waisel *et al.* (1970) could be due to different plant species or varieties, different electron microprobe techniques, pH of the medium, or perhaps a difference in the behavior of cationic and anionic Al in plants. However, Jones (1961) found that both forms produced P deficiency in some plants.

Rios and Pearson (1964) found that cotton grown with 2.5 ppm Al (but no P) in the subsurface solutions of a soil-nutrient solution split medium had a higher P concentration than those grown without Al. This suggested that P absorbed from the soil above moved downward and was precipitated by Al absorbed from the nutrient solution. This could have implications regarding P fertilizer efficiency in soils having Al toxic subsurface layers.

Aluminum is known to reduce hexose phosphorylation (Rorison, 1965; Clarkson, 1966b, 1969), the process by which P from ATP combines with sugars to give sugar phosphates and ADP (catalyzed by hexokinases). Clarkson (1966b) showed further that Al citrate inhibited the activity of a purified yeast hexokinase, reduced the rate of sugar phosphorylation by crude mitochondrial extracts from barley roots, and increased concentrations of ATP in barley roots. Woolhouse (1969) has noted that Al inhibits adenosine triphosphatases in plants, and this led Clarkson (1969) to conclude that Al acts directly or indirectly to prevent the utilization of ATP in glucose phosphorylation.

In summary, the biochemical evidence indicates that Al binds P on root surfaces and cell walls and in the free space of plant roots (Rorison, 1965; Clarkson, 1966b, 1967a), making P less available to metabolic sites within the cells. Some of the Al absorbed by plant roots also appears to penetrate the cells of meristematic tissue and to interfere with cell division, respiration, DNA synthesis, and sugar phosphoryla-

tion (Rorison, 1965; Clarkson, 1966b, 1969; Norton, 1966–67; Sampson *et al.*, 1965).

4. Effects of Aluminum on Rhizobia

Very little information is available concerning the direct effects of the Al ion on rhizobia. MacLeod and Jackson (1965) cited the work of Kliewer (1961), who reported that 0.4 to 0.7 ppm Al in solution greatly reduced the effective nodulation of birdsfoot trefoil (*Lotus corniculatus*). No other references were found on the subject.

III. DIFFERENTIAL ALUMINUM TOLERANCE OF PLANT SPECIES AND VARIETIES

A. Range of Tolerance

Plant species differ widely in their tolerance to excess soluble or exchangeable Al in acid soils or nutrient solutions (McLean and Gilbert, 1927; Lignon and Pierre, 1932; Hewitt, 1948; Jones, 1961; Foy and Brown, 1964; Clarkson, 1966a; Jackson, 1967; Grime and Hodgson, 1969; Adams and Pearson, 1970). McLean and Gilbert (1927) classified lettuce, beets, timothy (*Phleum pratense*), and barley as Al sensitive; radishes, sorghum, cabbage, oats, and rye as medium sensitive; and corn, turnips, and redtop as resistant. Aimi and Murakami (1964) found that lettuce was more sensitive to Al in solution than turnips and radishes were; these in turn were more sensitive than maize, rice, cucumber (*Cucumis sativus*), and squash (*Cucumis* sp.). Aluminum tolerance in nutrient solution was well correlated with acid soil tolerance. Jones (1961) rated barley as Al sensitive; brussels sprouts (*Brassica oleracea*) and peas (*Pisum* sp.) as semitolerant; and S-100 white clover, mangold, mustard, and *Atriplex hastata* as tolerant. In general, plants classified as calcifuges (acid-soil plants), such as *Deschampsia flexuosa* and *Carex demissa*, are more tolerant to Al than those classified as calcicoles (calcareous-soil plants), such as *C. lepidocarpa* (Clymo, 1962; Grime and Hodgson, 1969).

The tomato (*Lycopersicon esculentum*) plant is very sensitive to Al and has been suggested as an indicator of Al availability in soils (Rees and Sidrak, 1956; Mercado and Velasco, 1961). The datura plant is much more tolerant than tomato or eggplant (Otsuka, 1968b). Alfalfa and cotton are injured by as little as 0.5 ppm Al in nutrient solutions or displaced soil solutions (Rios and Pearson, 1964; MacLeod and

Jackson, 1965). Buckwheat (*Fagopyrum esculentum*) is much more tolerant than barley or cotton (Foy and Brown, 1964). Cotton root growth was practically stopped in Al-toxic subsoils, which had no effect on peanut roots (Adams and Pearson, 1970). Perennial ryegrass, white clover, and subclover (*Trifolium subterraneum*) are reportedly unaffected by Al toxicity at soil pH values where alfalfa is severely injured.

The cranberry plant appears extremely tolerant to Al, requiring 150 ppm Al added to solutions (at pH 3.5) for reduction of shoot growth (Medappa and Dana, 1970). Root length tended to be reduced at Al concentrations above 2.5 ppm, but root weight was not seriously decreased by 25 ppm Al.

In acid soils Kamprath (1970) found that corn made good growth at Al saturations of up to 44% but soybeans (*Glycine max*) would not tolerate above 20%. Evans and Kamprath (1970) reported that corn responded to liming when the soils contained above 0.4 meq Al/100 g and soybeans above 0.2 meq/100 g, corresponding to Al concentrations of 3.6 and 1.8 ppm in displaced soil solutions. Clarkson (1966a) found that species of the *Agrostis* (bentgrass) genus differed widely in Al tolerance. Roots of *A. stolonifera* showed injury at 5.4 ppm Al and *A. canina* at 10.8 ppm, but those of *A. setacea* and *A. tenuis* showed no root damage at 21.6 ppm Al in nutrient solution. Furthermore, *A. setacea* grew at 43.2 ppm Al, which inhibited root growth of *A. tenuis*.

The Al tolerance ratings of the species given above can only be considered estimates of the range of tolerance available in plants. The tolerance of a specific plant to a given amount of Al added to a culture is determined by many factors (pH, Ca, P, plant variety, and so on), which probably varied in the experiments cited.

Plant varieties within species also differ widely in Al tolerance, and this is partly responsible for the different species rankings in the older literature. Such varietal differences have been found in wheat and barley (Neenan, 1960; Foy *et al.*, 1965a, 1965b, and 1967; MacLean and Chiasson, 1966; Kerridge *et al.*, 1971), alfalfa (Ouellette and Dessureaux, 1958), perennial ryegrass (Vose and Randall, 1962), soybeans (Foy *et al.*, 1969), rice (Ota, 1968), Irish potatoes (Lee, 1971a, 1971b), and peanuts (Adams and Pearson, 1970). Lee (1971b) rated the Al tolerance of potato varieties as: Netted Gem (Russet Burbank) > Katahdin > Sebago > Green Mountain. Netted Gem actually seemed to require 1 to 5 ppm Al in the nutrient solution for best vegetative growth. Katahdin benefited from 1 ppm Al but was seriously injured by 5 ppm. Sebago was not affected by 1 to 5 ppm Al, and 10 ppm were required for injury. The Green Mountain variety was sensitive to 1 ppm Al. For additional details on species and varietal

differences in Al tolerance, see tables in Jackson (1967) and Adams and Pearson (1967). Varietal differences in tolerance to acid, Al-toxic soils are illustrated for wheat (Table 20.3), barley (Fig. 20.1), and soybeans (Table 20.4). Differential Al tolerance of two barley varieties in nutrient solution is shown in Figure 20.2.

B. Characterization of Differential Aluminum Tolerances among Plant Species and Varieties

The exact biochemical nature of Al toxicity is still debated. Morphological, physiological, and biochemical properties, which have been associated with differential Al tolerance, are summarized here.

Table 20.3. Differential lime response of three wheat varieties on Al-toxic Tatum soil

CaCO ₃ added (ppm)	Average soil pH	Yield of plant tops (g/pot)†		
		Atlas 66	Monon	Thatcher
0	4.2	1.50 a	0.49 c	0.23 d
1500	5.1	4.23 a	3.66 a	3.71 a
3000	5.8	4.25 b	4.66 a	4.76 a
4500	6.7	3.67 a	3.95 a	3.99 a
6000	7.2	3.16 a	2.99 a b	2.81 a b c

Source: Foy *et al.*, 1965a.

† Within a given lime level yield values having a letter in common are not significantly different at the 5% level by the Duncan Multiple Range Test. Origins of varieties are: Atlas 66, N.C.; Monon, Ind.; and Thatcher, Minn.

Table 20.4. Yields of tops of four soybean varieties on Al-toxic Bladen surface soil at different lime levels

CaCO ₃ added (ppm)	Final average soil pH	Yield of plant tops (g/pot)†				
		Wayne	Clark	PI 85666	Perry	Chief
0	4.7	4.37 b c	3.63 e f	2.91 g	4.28 b c	3.26 f g
1500	5.0	5.39 b c	5.39 b c	4.84 c d e	5.38 a b c	5.31 b c d
3000	5.5	5.29 b c	5.32 b c	5.38 a b c	5.51 a b c	5.11 b c d
6000	6.4	4.67 c d	4.79 b c d	5.31 b c d	5.39 a b c	5.09 b c d

Source: Armiger *et al.*, 1968.

† Within a given lime level any two yields having a letter in common are not significantly different at the 5% level by the Duncan Multiple Range Test.

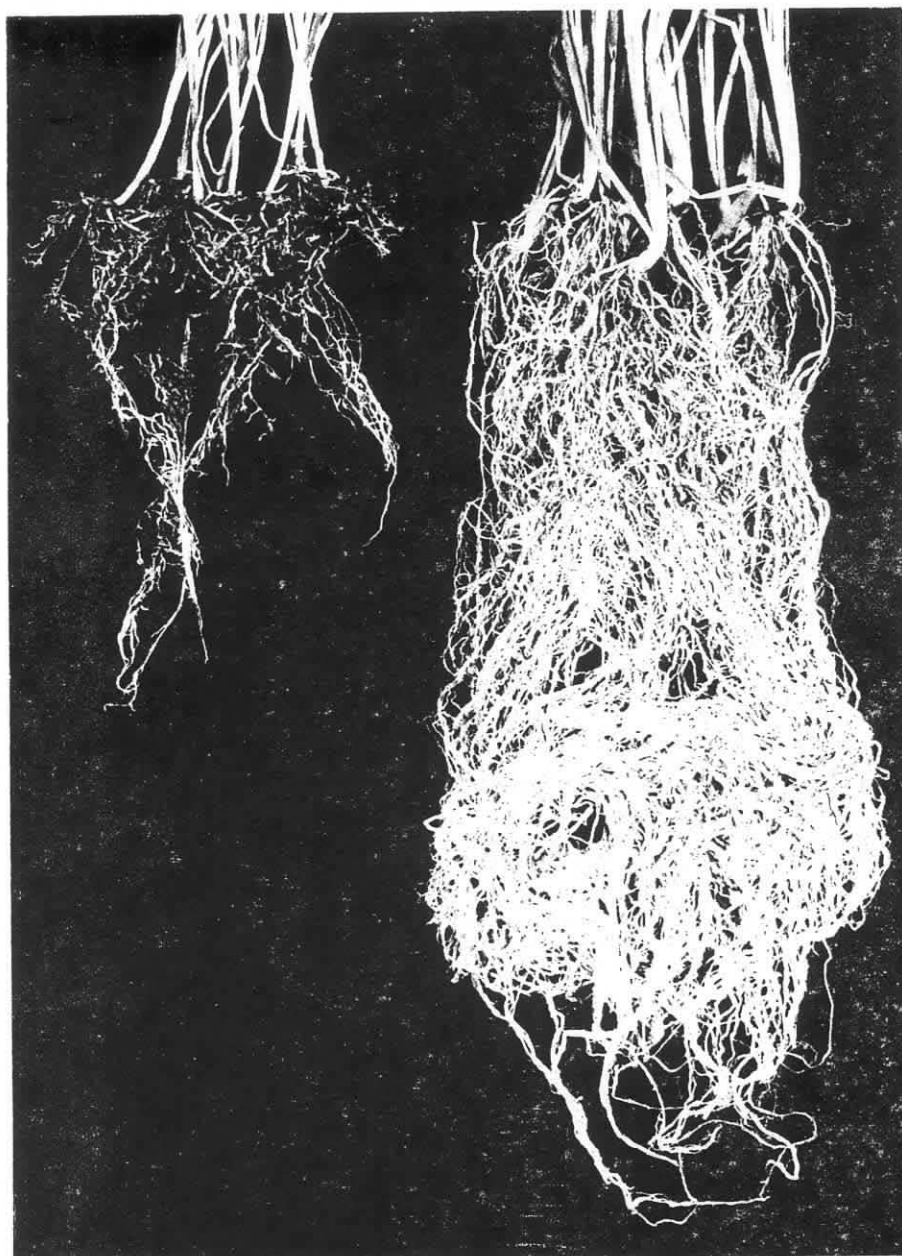


Fig. 20.1. Roots of Kearney (*left*) and Dayton (*right*) barley varieties grown in acid, Al-toxic Bladen soil (initial pH 4.6). (C. D. Foy, unpublished data)

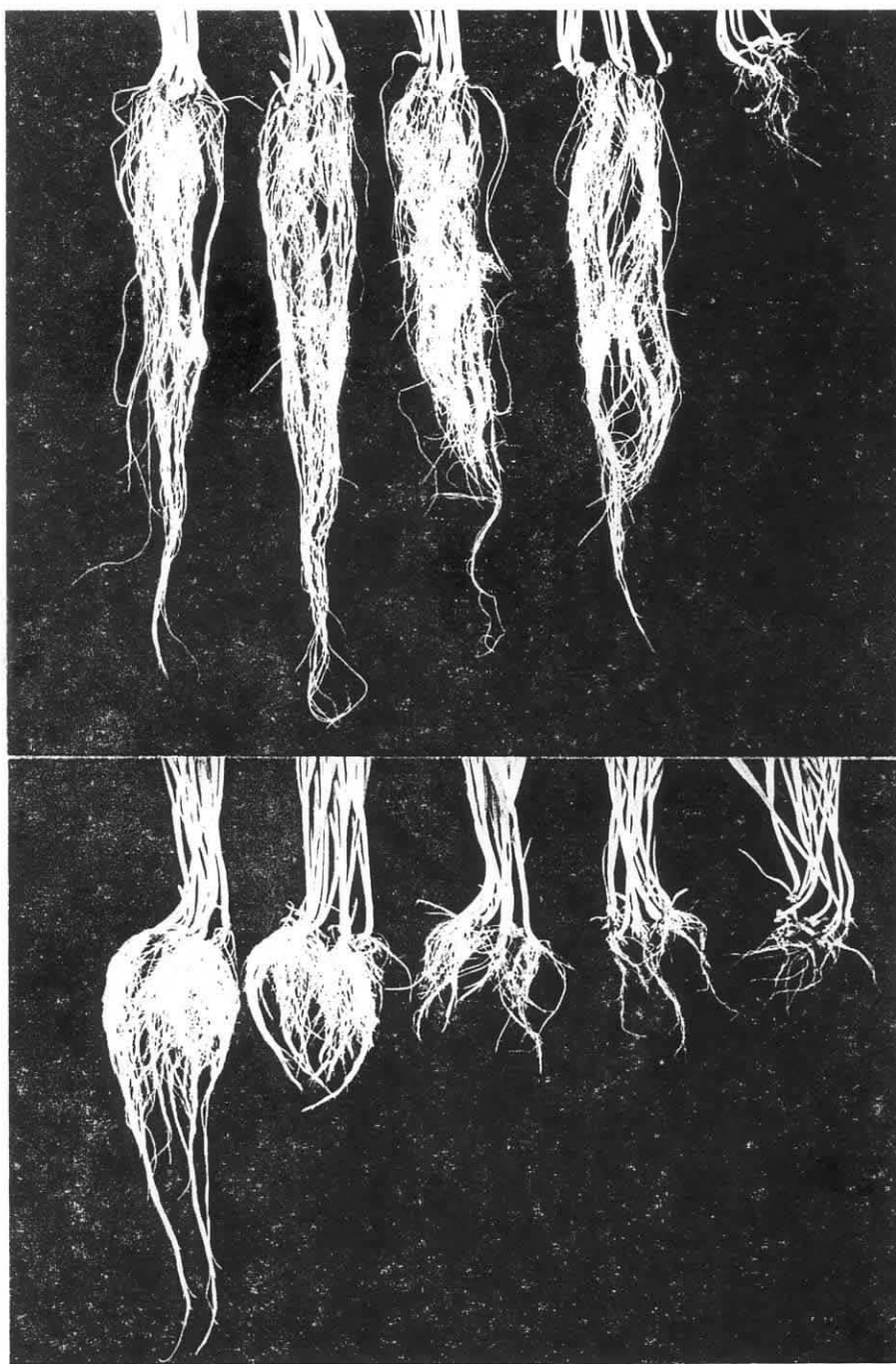


Fig. 20.2. Differential Al tolerance of Dayton (*top*) and Kearney (*bottom*) barley varieties in nutrient solutions. *Left to right*: 0, .75, 1.5, 3.0, and 6.0 ppm Al added at initial pH 4.8. Final pH values were 6.8, 7.0, 7.2, 6.7, and 4.4 for Dayton and 7.2, 6.6, 6.2, 4.7, and 4.4 for Kearney. (Foy *et al.*, 1967)

1. Root Morphology

Fleming and Foy (1968) found that greater Al tolerance in Atlas 66 wheat compared with Monon was associated with greater ability to continue root elongation and resist morphological damage to root tips and lateral roots when under Al stress and to initiate new lateral roots when the stress was removed. Differential Al tolerance of Atlas 66 and Monon wheat roots are shown in Figures 20.3 and 20.4. In addition, the greater Al injury in the more sensitive Monon variety was characterized by greater internal disorganization and the appearance of binucleate cells in roots. Reid *et al.* (1971) showed that Al injury in barley varieties is characterized by an increase in the numbers of roots, a decrease in root length and root weight per plant, and inhibition and darkening of root tips and laterals (Table 20.5).

2. Plant-induced pH Changes in Root Zones

Differential Al tolerance among some plant species and varieties is associated with differential ability to alter the pH of their root zones. For example, Foy *et al.* (1965b, 1967) showed that Al-sensitive Monon wheat and Kearney barley varieties induced lower pH values in their growth media than did the Al-tolerant Atlas 66 wheat and Dayton *Table 20.5.* Differential effects of aluminum on root characteristics of barley varieties in nutrient solutions and in Al-toxic Tatum soil.

Variety	Nutrient solution† (4 ppm Al/no Al %)			Tatum soil (low lime/high lime %)
	No. of roots per plant	Max. root length	Root wt. per plant	Root wt. per pot
<i>Al-tolerant</i>				
Colonial 2	117	62	159	77
Calhoun	115	63	168	89
Dayton	110	70	149	75
Barsoy	109	74	143	108
<i>Al-sensitive</i>				
Cordova	207	17	67	53
Kenbar	190	17	79	62
Kearney	165	9	44	29

Sources: Nutrient solution data adapted from Reid *et al.*, 1971; Tatum soil data from Reid *et al.*, 1969.

†Nutrient solutions contained 3 ppm P; pH was adjusted initially to 4.8 and twice daily thereafter for the growth period of 18 days.



Fig. 20.3. Effects of Al on primary root tip structure in Atlas 66 (*left*) and Monon (*right*) wheat varieties, with no Al (*top*) and 9 ppm Al (*bottom*) added. (Fleming and Foy, 1968)

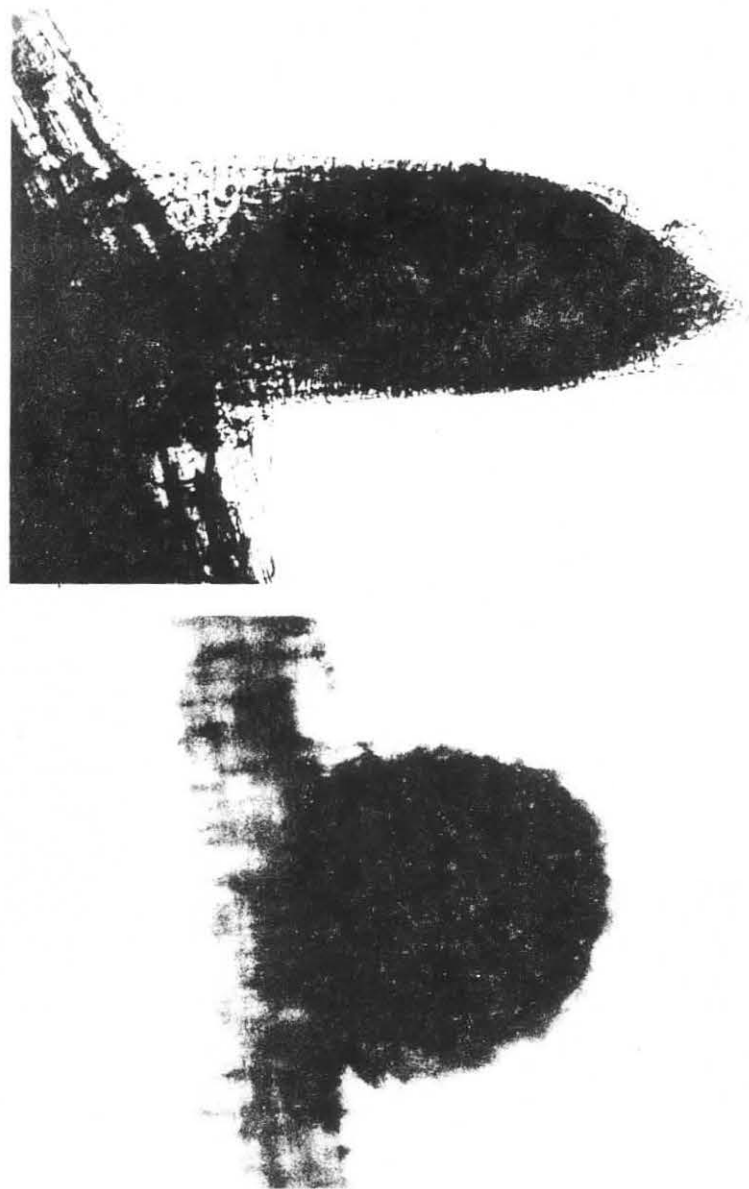


Fig. 20.4. Differential effects of 9 ppm Al on lateral root structure in Atlas 66 (*top*) and Monon (*bottom*) wheat varieties. (Fleming and Foy, 1968)

barley varieties (Table 20.6). Because a lower plant-induced pH in the root zone increases the solubility and potential toxicity of Al, this is an adequate beginning explanation for the differential Al tolerance of these varieties. In support of this hypothesis, Clarkson (1970) observed that when the nutrient solution pH was maintained at 4.2, Dayton and Kearney barley varieties appeared equally sensitive to Al. Otsuka (1968c) reported that an Al-tolerant wheat variety (Hiracki) raised the pH of its growth medium, but an Al-sensitive variety (Norin 25) lowered it. Rice seeds from acid-soil-tolerant (probably Al-tolerant) varieties raised the soil pH from 3.2 to 5.5 during germination, but those from acid-soil-sensitive varieties did not (Subramoney and Saukaranarayanan, 1964). Greater Al sensitivity of cotton compared with peanuts in acid subsoils has also been associated with the creation of a more acid root environment (Adams and Pearson, 1970). Chamura and Koike (1960) found that the pH of plant roots grown in culture solutions increased with increasing acid resistance in the order: rice > tobacco > maize > mint > sorghum.

Wilkinson (1970) has discussed some possible causes of pH lowering in plant root zones: (1) hydrogen ion release as a result of excess cation over anion absorption; (2) release and hydrolysis of CO_2 ; (3) release of H ion from carboxyl groups of polygalacturonic acid residues of pectic acid (which would result in the higher CEC values found in Al-sensitive wheat and barley varieties, which lower the pH more than Al-tolerant varieties); and (4) excretion of protons from microorganisms associated with roots. Pitman (1970) noted that H ion loss from excised, low-salt barley roots appeared to be coupled to phase II salt uptake and was not due to increased respiration or metabolic breakdown of sugars. Because of the large net negative potential (-60 mV) observed, he suggested that H ion loss is due to an active outward proton transport. He also pointed out that the efflux of organic acids, OH ions, or HCO_3 ions will increase or decrease the apparent H release. Riley and Barber (1969) attributed increase in pH and HCO_3 in soybean root zones to greater uptake of anions (particularly NO_3) than cations. In a more recent study Riley and Barber (1971) found that on a soil having an initial pH of 5.2, the final pH in the rhizocylinders of soybeans fertilized with $\text{NH}_4^+\text{-N}$ was decreased to 4.7 but that in the root zone of plants fertilized with $\text{NO}_3^-\text{-N}$, the pH was increased to 6.6.

Differential Al tolerances between Perry and Chief soybean varieties (Foy *et al.*, 1969) and Dade and Romano snapbean varieties (Foy *et al.*, 1972) do not appear to be associated with differential pH changes in nutrient cultures. This may mean that in some plants differential pH changes are merely results, rather than primary causes, of differential Al

Table 20.6. Differential Al tolerance of Dayton and Kearney barley varieties in relation to pH changes in nutrient solutions and composition of plant tops

Barley variety	Al added (ppm)	Final solution pH†	Plant composition (meq/100 g)						
			Plant yield (g/pot)‡		Tops			Roots	
			Tops	Roots	Al	H ₂ PO ₄	Ca	Al	H ₂ PO ₄
Dayton	0	6.8	2.41	0.81	4.5	20.2	28.2	2.4	18.7
Kearney	0	7.2	3.19	1.07	4.4	20.7	48.8	3.8	20.0
Dayton	3	6.7	2.20	0.84	5.0	10.0	27.4	20.6	13.8
Kearney	3	4.7	2.40	0.22	4.5	15.8	12.4	35.3	21.5

Source: Foy *et al.*, 1967.

† pH initially adjusted to 4.8 and left unadjusted thereafter.

‡ Yields of 16 plants grown for 20 days in 9 l of solution.

tolerance. Because pH affects so many aspects of soil chemistry and plant nutrition, this subject deserves much more exhaustive study.

Small and Jackson (1949) reported that the root sap of oats (rather tolerant to acid soils and Al) had a higher buffer capacity (within the pH ranges of 4.6 to 4.8 and 6.4 to 6.6) than barley, which is more sensitive to these conditions. Ikeda (1965) also associated the higher Al tolerance in certain wheat varieties with higher buffer indexes of root sap. Chenery (1948) noted that the pH of cell sap from Al-accumulating plants was generally below 5.3. The significance of such information is not immediately apparent in explaining differential Al tolerance, but the subject should receive further study in relation to Al mobility in plant sap and the interactions of Al with root exudates in soils.

3. Aluminum Uptake and Transport

Aluminum tends to accumulate in the roots but not in the tops of some Al-injured plants (MacLeod and Jackson, 1965; Foy *et al.*, 1967). Rorison (1958) found that the inhibition of alfalfa root elongation by Al was associated with a rapid Al uptake and suggested that tolerant plants might take up Al more slowly. Aluminum concentrations in plant roots are often negatively correlated with crop yields on acid soils (Chamura, 1962; Ota, 1968). Rorison (1965) found that Al movement into excised roots of sanfoin (*Onobrychis sativa* Lam.) followed a normal curve which suggested little uptake into nonfree space. Clarkson (1967a) found most of the Al in Al-injured barley roots to be associated with the cell walls.

Differences in Al tolerance among wheat, barley, and soybean varieties have not been associated with differential Al concentrations in plant tops (Table 20.6; Foy *et al.*, 1967, 1969a). Aluminum-tolerant varieties of perennial ryegrass, wheat, and barley have lower root cation exchange capacities and accumulate lower concentrations of Al in their roots than do sensitive varieties (Vose and Randall, 1962; Foy *et al.*, 1967). However, the Al-tolerant Perry soybean variety did not accumulate any less Al in its roots than did the Al-sensitive Chief variety (Foy *et al.*, 1969).

Some investigators have reported that Al concentrations in plant tops correlate with Al injury. Otsuka (1968a) observed that Al-tolerant Hiracki wheat contained a lower Al concentration in its shoots than did the Al-sensitive Norin 25 variety. Ouellette and Dessureaux (1958) found that Al-tolerant alfalfa clones contained lower concentrations of Al in their tops and higher concentrations of Al in their roots than did Al-sensitive clones. Lunt and Kofranek (1970) observed that the

azalea (*Rhododendron*) plant, which is quite tolerant to Al, retains 90% of its total Al content in the roots. Other plants that appear to tolerate Al by excluding it from their tops are cranberry (Medappa and Dana, 1970) and pangolagrass (*Digitaria decumbens* Stent.) (Moomaw *et al.*, 1959).

Hoyt and Nyborg (1971) found that Al concentrations in alfalfa tops grown on acid Canadian soils (pH 4.0 to 5.6) were highly correlated with Al extracted from soils by 0.01 M CaCl_2 and with Al activity calculated by the Debye-Huckel method but less well correlated with that extracted by 0.002 N HCl or ammonium acetate at pH 4.8. Salt-extractable Al was also significantly correlated, but to a lesser extent, with alfalfa yield response to lime. In these studies the Al contents of alfalfa were only 44 to 134 ppm, which are well below the 200 to 325-ppm critical range established by Ouellette and Dessureaux (1958) for alfalfa injury.

In some plants Al tolerance is associated with accumulation of Al in the tops, rather than exclusion from tops and/or roots. Hu *et al.* (1957) reported that plants which are indicative of acid soils in China usually had lower concentrations of Ca, P, Na, K, and Fe and higher concentrations of Mn and Al than calcareous-soil plants. Jones (1961) found that Al-tolerant plant species, such as *Atriplex hastata*, took up more Al than Al-sensitive species, such as barley. Suchting (1948) noted that pine trees, which are noted for acid soil and Al tolerance, accumulated 1,000 to 1,500 ppm Al in the tops when grown on an acid soil and only 200 to 450 ppm when grown on a sand-humus medium. Mangrove (*Rhizophora horisonii*) is also reported to be an Al accumulator (Hesse, 1963). Moomaw *et al.* (1959) found that 13 of 23 Hawaiian plant species contained more than 1,000 ppm Al in their tops and were classified as Al accumulators. Staghorn fern (*Gleichenia linearis* Burm, C. B. Clarke) appeared to be an obligate accumulator of Al and a fair indicator of bauxite deposits. In such plants Al may be prevented from reaching critical metabolic sites within the cells (trapped in cell walls), or enzymes may be altered to tolerate Al (Turner, 1969).

4. Calcium Uptake and Use

Differential Al tolerance among varieties of several plant species and varieties appears to be closely associated with the differential uptake and transport of Ca. Aluminum-sensitive wheat and barley varieties are more susceptible to Al-induced Ca deficiency than are tolerant varieties (Foy *et al.*, 1967, 1969; Long and Foy, 1970). Table 20.6 shows that Al inhibits Ca uptake to a greater extent in Al-sensitive

Kearney barley tops than in those of Al-tolerant Dayton. Perry soybeans are more tolerant to Al in acid Bladen soil and in nutrient solution than is the Chief variety. Greater Al sensitivity of the Chief variety is associated with greater susceptibility to a petiole collapse which was identified as an Al-induced Ca deficiency in the actual zone of collapse. Chief is also more susceptible to a cupping symptom in young leaves which has been observed in plants grown on Bladen subsoil (Armiger *et al.*, 1968). Aluminum treatment reduced Ca concentration in roots and tops of Al-sensitive Chief to a greater degree than in those of Al-tolerant Perry. Differential Al tolerance between the two varieties was greater with 2 ppm Ca (Fig. 20.5) than with 50 ppm (Fig. 20.6) in the solutions. Note in Figure 20.5 that with low Ca (2 ppm), adding Al induces a coralloid root structure, which is quite different from that at higher Ca levels (50 ppm) shown in Figure 20.6. Note also in Figure 20.5 that Perry can produce a fibrous root at higher Al levels than Chief.

Ouellette and Dessureaux (1958) found that Al-tolerant alfalfa clones contained lower concentrations of Al in their tops and higher concentrations of Al and Ca in their roots than did Al-sensitive clones. They suggested that Ca reduced Al toxicity by reducing Al uptake and transport to plant tops.

5. Magnesium, Potassium, and Silicon Uptake

Greater Al sensitivity in sorghum compared with corn has been associated with a greater reduction in K uptake (Chamura and Hoshi, 1960). Effects of Al on K uptake were greater in young than in old plants. Lee (1971b) suggested that the greater Al tolerance in certain varieties of Irish potatoes is associated with the abilities of plant roots to absorb Mg and K. Ota (1968) found that rice varieties having the greatest resistance to bronzing (Al toxicity) have much higher levels of Si in the epidermal cells of leaves than do susceptible varieties. Silicon is known to reduce the internal toxicity of Mn in barley leaves (Williams and Vlamis, 1957) and may play a similar role in detoxifying Al. Silicon may also complex Al in soils and reduce its toxicity. Mattson and Hester (1933) showed that the addition of silicates to strongly acid soils lowered the soil pH at which plants were injured.

6. Phosphorus Uptake and Metabolism

Differential Al tolerance among certain plant species and varieties has been correlated with differential abilities to absorb and utilize P in

the presence of Al. For example, Al-tolerant buckwheat absorbs P much more effectively in solutions containing Al than does Al-sensitive barley (Foy and Brown, 1964). Abilities of plant species to tolerate high levels of anionic (aluminate) Al in alkaline fly ash deposits are also associated with abilities to maintain their P status (Rees and Sidrak, 1956; Jones, 1961). Hackett (1967) observed that *Deschampsia flexuosa*, which colonizes acid soils of pH 3.5 to 5.0, was much more tolerant to low P levels than perennial ryegrass, which is less tolerant to acid soils and Al. Clarkson (1967b) found that higher Al tolerance in *Agrostis setacea* compared with *A. canina* and *A. stolonifera* was associated with greater tolerance to low absolute levels of P in the growth medium. Otsuka (1968a, 1968b) reported that the greater acid soil and Al tolerance of datura compared with tomato and eggplant were associated with greater ability to absorb P in the presence of Al, or at low P levels in the absence of Al. Cranberry, which is extremely tolerant to acid soils and Al, can maintain normal P concentrations in its tops when grown with Al concentrations ranging from 2.5 to 150 ppm (pH 3.5) in the nutrient solution (Medappa and Dana, 1970). The detoxification of Al by synthetic chelating agents is closely associated with increases in the P concentrations of plant tops, in addition to growth increases (Rees and Sidrak, 1961; Foy and Brown, 1964). In the latter reference EDDHA [ethylenediamine di(o-hydroxyphenylacetic acid)] also decreased the Al concentration in plant tops and roots. Ikeda *et al.* (1965) noted a correlation between acid soil tolerance and tolerance to low P levels in wheat varieties.

MacLean and Chiasson (1966) found that Al-induced reductions in the P concentrations of plant tops and increases in those of plant roots were more pronounced in Al-sensitive Herta barley than in Al-tolerant Charlottetown 80. Goodman (1969) stated that P seems to be the most important major nutrient in determining the ecological distribution of plants. Foy *et al.* (1965b, 1967) found that the tops of Al-sensitive Monon wheat contained lower concentrations of P than the tops of the Al-tolerant Atlas 66 when both were grown on Al toxic soil. However, this was not consistently true for plants grown in nutrient cultures. Aluminum-sensitive Kearney barley tops and roots contained higher P concentrations than those of Al-tolerant Dayton when both were grown with Al in nutrient cultures (Foy *et al.*, 1967). There is a possibility, however, that Al affects P metabolism differently in the two varieties. This question merits further study.

In contrast to the evidence presented above, Ouellette and Dessureaux (1958) concluded that differential Al tolerance among alfalfa clones was not due to Al-P interactions. In this same vein, Clarkson (1966a) reported that P deficiency symptoms in shoots of *Agrostis*

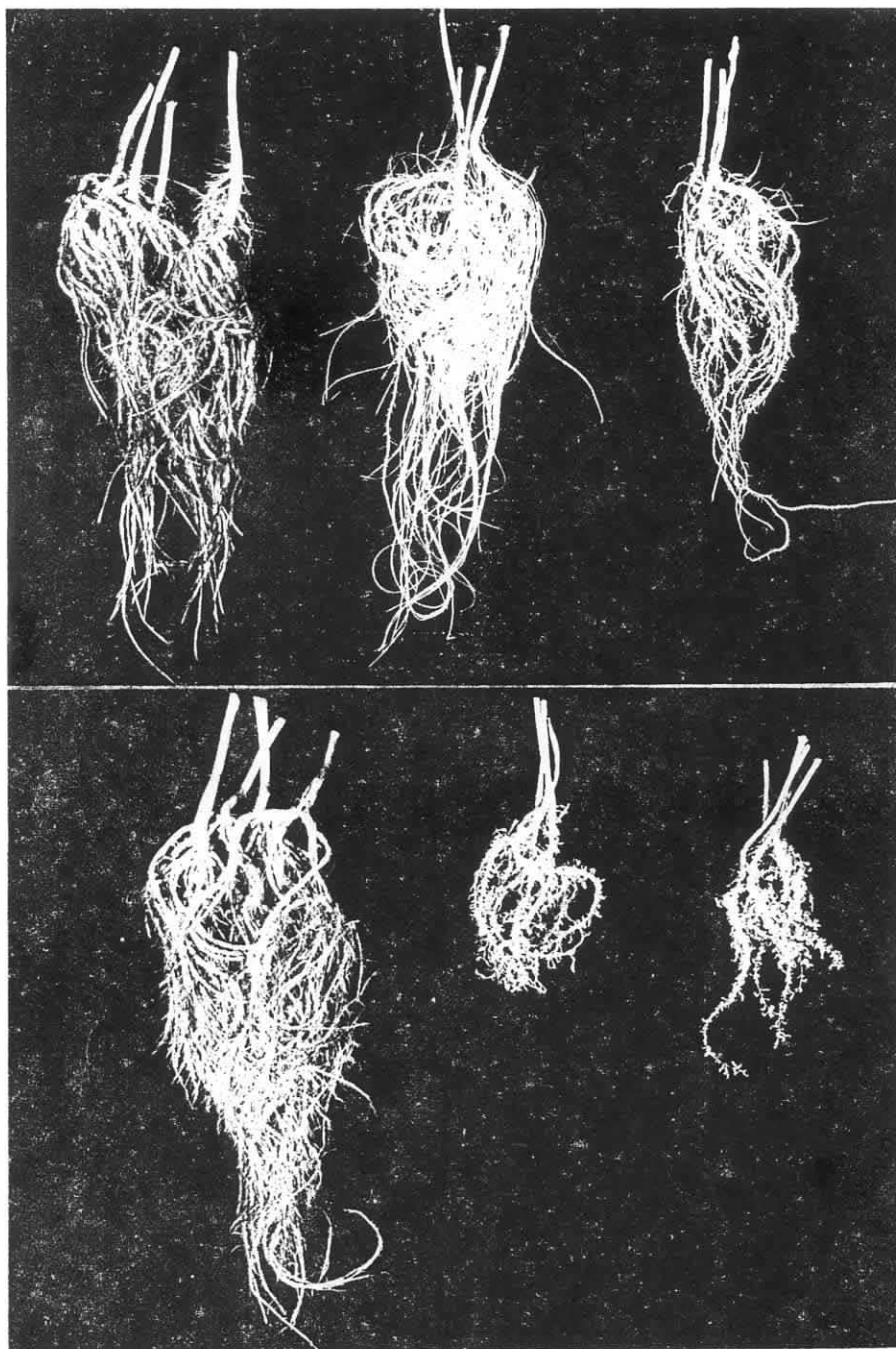


Fig. 20.5. Differential Al tolerance of Perry (*top*) and Chief (*bottom*) soybean roots with 2 ppm Ca in the nutrient solution. *Left to right*: 0, 8, and 12 ppm Al added. (Foy *et al.*, 1969)

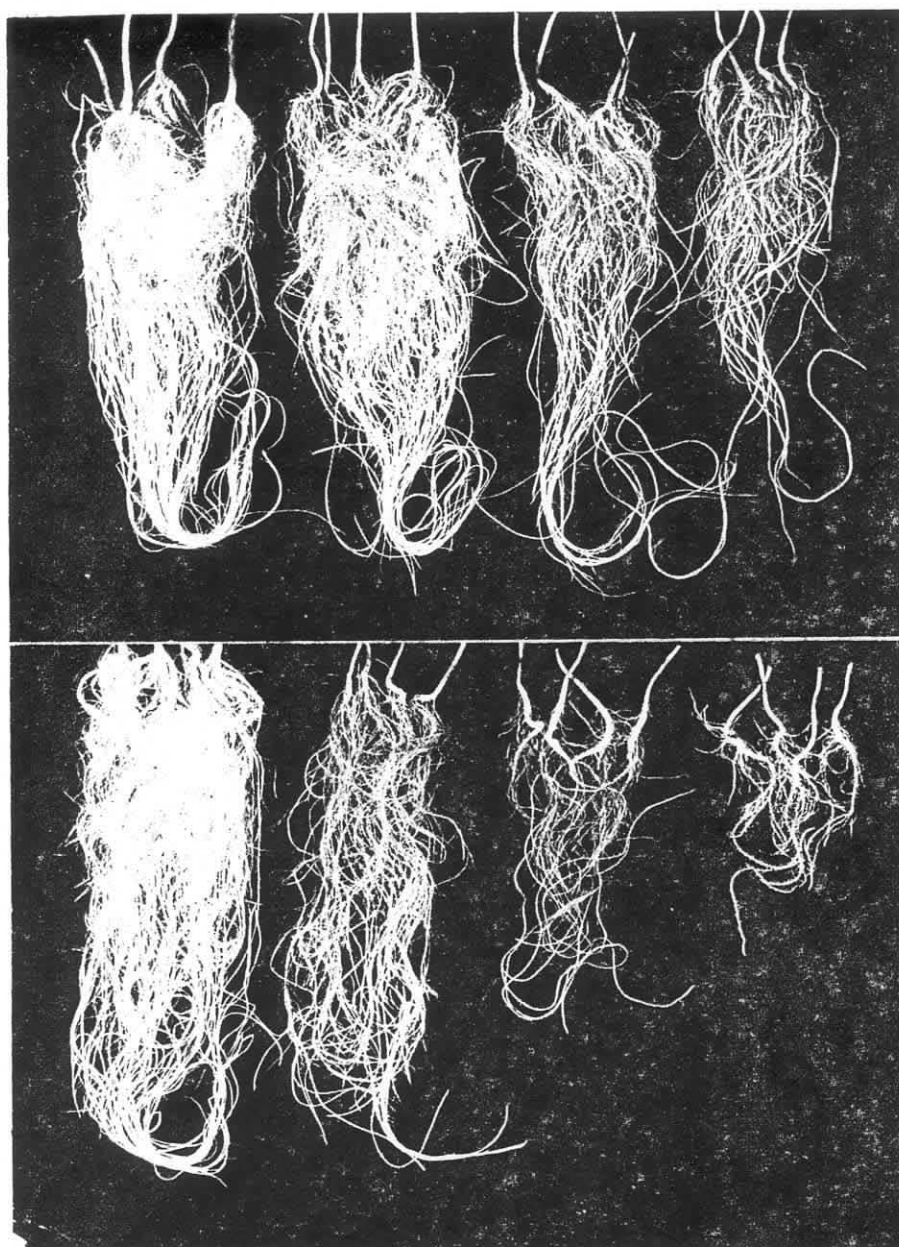


Fig. 20.6. Differential Al tolerance of Perry (*top*) and Chief (*bottom*) soybean roots with 50 ppm Ca in the solution. *Left to right*: 0, 8, 10, and 12 ppm Al added. (Foy *et al.*, 1969)

canina, *A. stolonifera*, and *A. tenuis* were not correlated with root abnormalities produced by Al.

Jones (1961) suggested that organic acids in tolerant species chelate Al and thus prevent the Al-P precipitation that would normally occur in plants at physiological pH values. According to Small (1946), acidophilic plants generally have strong organic acid buffer systems in their cells, in contrast to alkaphiles, in which phosphate buffers dominate the system. However, the alkatoralant plants may have (1) a strong phosphate buffer system dominating a weak organic acid system or (2) a strong organic acid buffer system which can resist neutralization by an alkaline growth medium. Barley, which is sensitive to cationic Al at low pH and anionic Al at high pH, is known to have a phosphate type buffer system. In contrast, *Beta maritime*, which colonizes alkaline, aluminate-toxic fly ash deposits, has an organic acid buffer system. Such differences in plant buffer systems may be important in regulating Al-P interactions and in determining the differential Al tolerance of plant species and varieties (Jones, 1961).

In support of the chelation hypothesis of Al tolerance proposed by Jones (1961), Chamura and Koike (1960) reported that acid soil tolerance in several plant species was positively correlated with the citric acid contents of roots; however, the acid-soil-tolerant species had lower concentrations of citric and several other organic acids in their leaf blades than did the acid-soil-sensitive species. Some Al-tolerant species are known to accumulate high concentrations of Al in their tops, and many Al-sensitive plants accumulate Al in roots but not in tops. Such differences in Al mobility within the plant may partially explain the observed differences in Al toxicity. Clarkson (1966a) showed that Al in the cationic form inhibited cell division in adventitious roots of *Agrostis stolonifera* but chelated Al did not. Grime and Hodgson (1969) suggested that the Al resistance of certain calcifuge species is due to a chelating mechanism which also has an affinity for Fe. Johnson and Jackson (1964) found that Al-EDTA reduced Al uptake and increased Ca uptake by excised barley roots, when compared with AlCl₃ at pH 4.0.

A chelation mechanism for the detoxification of Al in tolerant species seems compatible with one hypothesis for explaining the differential P-fixing powers of plants. This hypothesis is that certain plant roots produce exudates that complex Fe and Al, reverse or prevent P fixation, and increase the availability of P to the plant (Drake and Steckel, 1955). Struthers and Sieling (1950) found that the naturally occurring organic acids (citric, oxalic, tartaric, malonic malic, and lactic) were effective in preventing the precipitation of Fe and Al in the pH range at which P fixation occurs in soils. For example, 1

millimole of citric acid completely complexed 1 millimole of Al and prevented P fixation over the pH range of 4 to 9. The efficiency of organic acids in this process increased with the number of carboxyl and functional hydroxyl groups and decreased with the length of the carbon chain. These investigators pointed out that such acids are produced in considerable quantities in soils during the microbial decomposition of organic matter. Harris (1961) suggested that plants absorb Al and return it to the soil, possibly in a chelated form.

Woodhouse (1969) found that the adenosine triphosphatase activity of cell wall preparation from roots of an acid soil ecotype of *Agrostis tenuis* was inhibited less by Al than was that of a preparation from a calcareous soil ecotype of the same species. He suggested the possibility that differential Al tolerances within this species are related to structural changes in these enzymes. In this connection, Bielecki (1970) has suggested that low P levels in root zones may induce the activity of acid phosphatases in roots and enable plants to extract P from organic forms such as phytin.

Clarkson (1969) has pointed out that the observed Al-induced inhibition of oxidative phosphorylation in plant roots should result in decreased respiration. Norton (1966-67) found that 54 ppm Al reduced respiration rates in Al-sensitive sanfoin roots by 5% within 30 minutes and by 35% within 3 hours after exposure, long before inhibited cell division was detected. Respiration rate in Al-tolerant lupine (*Lupinus luteus*) was not affected by the same treatment. In contrast, Clarkson (1969) found that in Al-sensitive onion roots the inhibition of cell division induced by Al occurred much earlier than the small reductions in respiration observed. Furthermore, the inhibition of cell division by Al did not seem to be affected by the presence or absence of P in the medium and could not be overcome by subsequent treatments with P for one week. He concluded that cell division was much more easily disturbed by Al than was general metabolism. Clarkson (1969) found that a 24-hour pretreatment with 27 ppm Al at pH 4.0 decreased respiration rates in the roots of four barley varieties. The decrease was 17% for Al-tolerant Dayton and 6% for Al-sensitive Kearney.

Aluminium is known to interfere with DNA replication in the mitotic cycle, fix P in inorganic form at root surfaces, reduce sugar phosphorylation, decrease respiration, and interfere with the uptake and utilization of Ca, P, and other elements and water. Such information suggests many fertile areas of research for identifying the physiological and biochemical processes responsible for differential Al tolerance in plant species and varieties. This information will, in turn, aid the plant breeder in tailoring plants to fit specific soil situations.

C. Breeding Aluminum-tolerant Plant Varieties

Because liming a soil to pH 5.5 to 6.0 will precipitate Al from solution, and eliminate its toxicity to plants, why not apply lime and forget about Al-tolerant varieties? Listed below are some acid soil situations in which liming may not be an adequate solution to the problem of Al toxicity.

1. Acid Subsoils

Excess soluble Al in acid subsoils reduces root proliferation and drought tolerance. Lime applied to surface soils does not move at a satisfactory rate, and liming the subsoil is difficult and generally not economically feasible. (Soil management practices are needed to prevent the further decrease of subsoil pH to values at which no plant can grow.)

2. Acid Surface Soils and Subsoils in Developing Countries

In many developing countries adequate liming will probably not be practiced for many years because of economic factors, such as lack of lime source, processing and transporting machinery, or suitable roads. In this connection Ikeda *et al.* (1965) has mentioned the necessity for having acid-soil-tolerant wheat and barley varieties for newly reclaimed lands on which adequate liming and P fertilization are not practiced for economic reasons. Ota (1968) proposed the adoption of Al-tolerant rice varieties in Ceylon to prevent bronzing.

3. Acid Surface Soils That Must Be Kept below pH 5.5

Chiasson (1964) has pointed out that most of the barley acreage in eastern Canada follows Irish potatoes. In this potato-barley rotation it is necessary to maintain the soil pH below about 5.4 to control the potato scab disease. However, at these pH levels Al is frequently soluble in toxic concentrations for the standard barley varieties used. The pH factor is so critical that good barley is sometimes produced at pH 5.4 and poor barley at 5.0. Aluminum injury is commonly expressed as a P deficiency symptom.

4. Acid Mine Spoils

Pyrites in acid mine spoils are oxidized to sulfuric acid, producing pH values as low as 2.5 to 3.0. In general, such spoils must be limed

to about pH 4.0 (or higher for legumes) to reduce H ion toxicity before plants can be grown. However, between pH 4.0 and about 5.5, toxicities of Al and perhaps other elements, such as Mn, and their interactions with essential elements may limit growth. It is often not economically feasible to apply sufficient lime to neutralize all of the harmful Al. Preliminary studies indicate that a good compromise in such cases is to lime the spoils to pH 4.0 to 4.5, to use plants with greater Al tolerance, and to fertilize with rock phosphate (USDA, 1971a, 1971b). The rock phosphate supplies P and Ca that may be needed, raises the soil pH somewhat, and probably also supplies sufficient soluble P to precipitate Al at a lower pH than can be accomplished with lime. Bradshaw (1970) suggested breeding plants for tolerance to excess lead, zinc, tin, and copper as the best possible approach in reclaiming mine wasteland contaminated with these metals.

In the acid soil situations mentioned above, we need crop species and varieties that can tolerate more Al than the standard varieties, extract P more effectively from Fe and Al compounds, and utilize Ca and P more efficiently in the presence of excess Al. In some cases greater tolerance to excess Mn is also needed. Present crop varieties that show some tolerance to Al are largely the indirect result of selecting for overall yield in the presence of various insect, disease, and climatic factors, with little attention to the soil. However, it is now clear that plant varieties reflect the surface and subsoil conditions under which they were developed. For example, wheat and barley varieties selected in North Carolina, where acid subsoils and Al toxicity are widespread, are generally more tolerant to Al than those selected in Kansas, where acid soils are less common. As another example, Ohio wheat and barley varieties apparently have been selected for higher Al tolerance than Indiana varieties (Foy *et al.*, 1965a). When varieties developed in one soil region are planted on slightly different soils within the same climatic zone, problems of toxicity or nutrient element deficiency may appear. Selecting plants more directly to fit the soil would reduce such problems.

In some plant species considerable progress has been made in breeding for increased Al tolerance. Dessureaux (1969) has studied methods for determining the genetic nature of differential Al tolerance among alfalfa clones. Reid (1971) found that Al tolerance in certain winter barley populations is controlled by a single dominant gene or factor, and he has developed methods for rapid screening of plants in soils and nutrient solutions in the greenhouse (see Table 20.5; Reid *et al.*, 1971). Aluminum tolerance determined in the greenhouse has been well correlated with grain yield on one acid, Al-toxic soil in the field (Reid *et al.*, 1969). The biochemical mechanism of such genetic control remains to be determined. Similar work on Al tolerance in

spring barley is being conducted in Canada (MacLean and Chiasson, 1966). Gorsline *et al.* (1968) postulated that three major genes regulate Al-Fe accumulation by certain corn inbred lines.

Kerridge and Kronstad (1968) concluded that at least one degree of Al tolerance in certain wheat populations was regulated by a single dominant gene. Kerridge *et al.* (1971) have developed a nutrient culture technique for separating degrees of Al tolerance within this species. Mesdag *et al.* (1970) have studied the possible genetic linkage between acid soil tolerance and protein content of wheat grain. Atlas 66 wheat, developed in North Carolina, has both high kernel protein content and high tolerance to soil acidity and Al. They concluded that these two traits are probably different genetically, although linked to some extent. Nevertheless, these investigators suggested the possibility of screening lines for soil acidity tolerance and selecting within segregating populations for high protein content in the kernel, provided that positive selection is used and that one parent combines both characteristics. Reid¹ has pointed out that there is no evidence to date that Al tolerance in winter barley is genetically linked with low absolute yield potential in the absence of Al. The Al tolerance trait can therefore be combined with other desirable plant characteristics.

The identification of physiological and biochemical plant properties associated with Al tolerance may provide useful screening tools for the plant breeder and increase our understanding of mineral nutrition in general. Sprague (1969) has emphasized that very little is known about the biochemical causes of differential yield potentials in plants. If we knew why plants adapt to certain soils, we could make more intelligent decisions about whether to change the soil to fit the plant, to change the plant to fit the soil, or to use a combination of the two approaches.

¹ D. A. Reid (USDA, ARS, Western Region, University of Arizona, Tucson, Arizona 85721), personal communication.

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